



ORIGINAL ARTICLE

How “The Blob” affected groundfish distributions in the Gulf of Alaska

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Abstract

We investigated the distributional shifts of groundfish in response to anomalous ocean conditions, particularly the recent anomalously warm period (2014–2016; “The Blob”), based on data from ten Gulf of Alaska bottom trawl surveys conducted by the Alaska Fisheries Science Center during 1996–2015. Six groundfish species were considered: Pacific cod (*Gadus macrocephalus*), arrowtooth flounder (*Atheresthes stomias*), walleye pollock (*Gadus chalcogrammus*), Pacific ocean perch (*Sebastes alutus*), northern rock sole (*Lepidopsetta polyxystra*), and southern rock sole (*Lepidopsetta bilineata*). Ontogenetic differences were examined by dividing data for each fish species into size classes. Our study demonstrated that after accounting for size-specific depth preferences, the spatial responses of groundfish to anomalous ocean conditions differed by species and foraging guild in the central Gulf of Alaska. Pacific cod and arrowtooth flounder showed similar responses to ocean warming, but different responses to cooling. In general, Pacific cod moved to deeper depths in warmer years and moved to shallower depths in colder years. Arrowtooth flounder also moved deeper in warmer years. However, in colder years, large arrowtooth flounder (>40 cm) shifted toward shallower depths while smaller-sized fish shifted toward deeper depths. In warmer years, large pollock (>30 cm) moved to deeper waters while smaller pollock (10–20 cm) moved to shallower waters. Pacific ocean perch exhibited an opposite response to thermal changes in habitat compared with Pacific cod and arrowtooth flounder. They moved deeper in colder years, but there was no clear change in depth as a function of size in response to warmer habitat.

KEYWORDS

arrowtooth flounder, bottom trawl survey, groundfish distributional shift, Gulf of Alaska, large marine heatwave, Pacific cod, walleye pollock

1 | INTRODUCTION

Marine ecosystems worldwide are experiencing increasing temperatures, changes in atmospheric forcing, circulation patterns, nutrient loads, and ocean acidity due to the impacts of anthropogenic-driven climate change (Kleisner et al., 2017; Nye, Link, Hare, & Overholtz, 2009; Root et al., 2003; Stock et al., 2011; Walther et al., 2002). Evidence of shifts in

distributions of fish stocks in response to climate variability has been observed (Barbeaux & Hollowed, 2018; Hollowed et al., 2012; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013). The magnitude of the shifts differs by species, life stage, and behavioral characteristics of the stocks (Barbeaux & Hollowed, 2018; Hollowed et al., 2012).

The processes underlying climate variability and change on larval survival have been studied for over a century. The mechanisms

underlying these changes are summarized in Bakun, Field, Redondo-Rodriguez, and Weeks (2010). In the Gulf of Alaska (GOA), recent studies have focused on the importance of larval drift and ecoregion connectivity in explaining age-0 settlement locations of groundfish populations (Hinckley, Parada, Horne, Mazur, & Woillez, 2016; Stockhausen, Coyle, Hermann, Blood, et al., 2018; Stockhausen, Coyle, Hermann, Doyle, et al., 2018). Although climate-induced shifts in the timing and location of spawning and larval distribution and survival could impact the spatial distribution of fish populations over time (Orensanz, Ernst, Armstrong, Stabeno, & Livingston, 2004; Parada, Armstrong, Ernst, Hinckley, & Orensanz, 2010), these early life history studies do not capture the short-term response of age-1+ fishes and the associated impacts of these changes on fisheries.

A marine heatwave of historic proportions occurred in the north-east Pacific Ocean during the period of 2014–2016 (“The Blob”; Bond, Cronin, Freeland, & Mantua, 2015). There are indications that the intensity of this marine heatwave was exacerbated by climate change (Walsh et al., 2018). For the upper 100 m of the ocean, an area of $\sim 2 \times 10^6$ km² was more than 2.5°C warmer than the long-term climatological mean (1981–2010) in early 2014, with peak anomalies exceeding 3 standard deviations. The development of this marine heatwave can be attributed to a strong and persistent blocking ridge of higher than normal sea-level pressure that was also associated with the worsening drought in California (Seager et al., 2015). It was accompanied by relatively low near-surface chlorophyll concentrations, presumably due to enhanced ocean stratification and, hence, reduced vertical mixing of nutrients (Whitney, 2015). From 2014 and into 2015, the upper ocean temperature anomalies became more prominent along the west coast of North America, extending from Baja California to the GOA. Upper ocean temperatures remained warmer than the long-term climatological mean through much of 2016, especially in the GOA and in the vicinity of the Alaska Peninsula. Extreme biological impacts occurred throughout the marine ecosystem from California to Alaska (Cavole et al., 2016).

Along with the anomalously warm ocean conditions in the GOA during 2014–2016, below-average fish conditions (i.e., lighter fish for a given length) were observed for several groundfish species including Pacific cod (Amar & Palsson, 2015) and walleye pollock (Dorn et al., 2016). A recent large population decline in the GOA Pacific cod stock likely resulted from increased post-larval stage mortality due to the combined effects of unusually warm waters in winter and limited forage (Barbeaux et al., 2017).

Here, we investigated the distributional shifts of groundfish in the GOA in response to anomalous ocean temperatures, including the 2014–2016 marine heatwave, using data collected from long-term Alaska Fisheries Science Center (AFSC) bottom trawl surveys. Six species were selected for analysis: Pacific cod (*Gadus macrocephalus*), arrowtooth flounder (*Atheresthes stomias*), walleye pollock (*Gadus chalcogrammus*), Pacific ocean perch (*Sebastes alutus*), northern rock sole (*Lepidopsetta polyxystra*), and southern rock sole (*Lepidopsetta bilineata*). The central GOA (CGOA) is characterized by a wide shelf incised by deep gullies and troughs, which is interrupted

by Kodiak Island (Figure 1). The western GOA (WGOA) has a much narrower shelf with fewer gullies, but it is also influenced by the Unimak Pass and other passes that connect the GOA with the Bering Sea. We excluded the eastern GOA (EGOA), due to insufficient sampling available for the analysis performed in this study. We focused on the CGOA where more than half of the bottom trawl survey stations were located. Our primary objective has been to evaluate the following hypotheses as responses to bottom temperature changes: (a) Groundfish that can tolerate a broad bathymetric range would move to deeper waters rather than shift their geographic ranges; (b) responses of shallow-water (<50 m) species would be less evident because they are better adapted to a wider range of seasonal variations in temperature.

2 | DATA AND METHODS

2.1 | GOA bottom trawl survey

Since 1984, the AFSC has conducted comprehensive bottom trawl surveys in the GOA during May–August to monitor the distribution, abundance, and biological characteristics of groundfish populations. The full area surveyed included the continental shelf and upper continental slope to a depth of 1,000 m, extending from the Islands of Four Mountains (52.9°N, 170°W) 2,300 km east to Dixon Entrance (54.7°N, 131.5°W; von Szalay & Raring, 2016; Figure 1). The AFSC sampled the standard 320,000 km² survey area with ~820 survey stations, triennially between 1984 and 1999, and biennially since 2001. The survey area was designed by using the former International North Pacific Fisheries Commission (INPFC) regions (von Szalay & Raring, 2016). Some of the INPFC survey areas directly correspond to the National Marine Fisheries Service (NMFS) reporting areas (e.g., Shumagin—610; Chirikof—620; and Kodiak—630). However, the INPFC Yakutat and southeastern areas divide at 137°W meridian, while the NMFS reporting areas Yakutat—640 and southeastern—650 divide at the 140°W meridian (von Szalay & Raring, 2016). Survey timing is consistent among years with chartered trawlers beginning in the WGOA in late May until late June and then operating in the CGOA from late June to July. The consistency of this timing is to minimize any seasonal changes in fish distributions due to spawning, foraging, or other factors.

The survey design is a stratified random design based upon depth, habitat type, and region, and the survey design has not been substantially altered since 1997. Survey stratification consisted of regions (WGOA and CGOA); sub-regions (typically east and west within a region); depth zones from 0–100 m, 101–200 m, 201–300 m, and 301–500 m; and habitat (shelf, slope, and gully). There were nine strata in the WGOA and 23 strata in the CGOA. Stations were selected at random within each stratum, and every haul was equally weighted. The number of stations was allocated among strata based upon the area of the stratum, and the past abundance estimates and variances of important commercial species. At each station, the vessel captain used a navigational depth sonar to locate seafloor that was sufficiently smooth enough to deploy and operate

GOA Bottom Trawl Survey, Bottom Temperature Anomaly, 2015

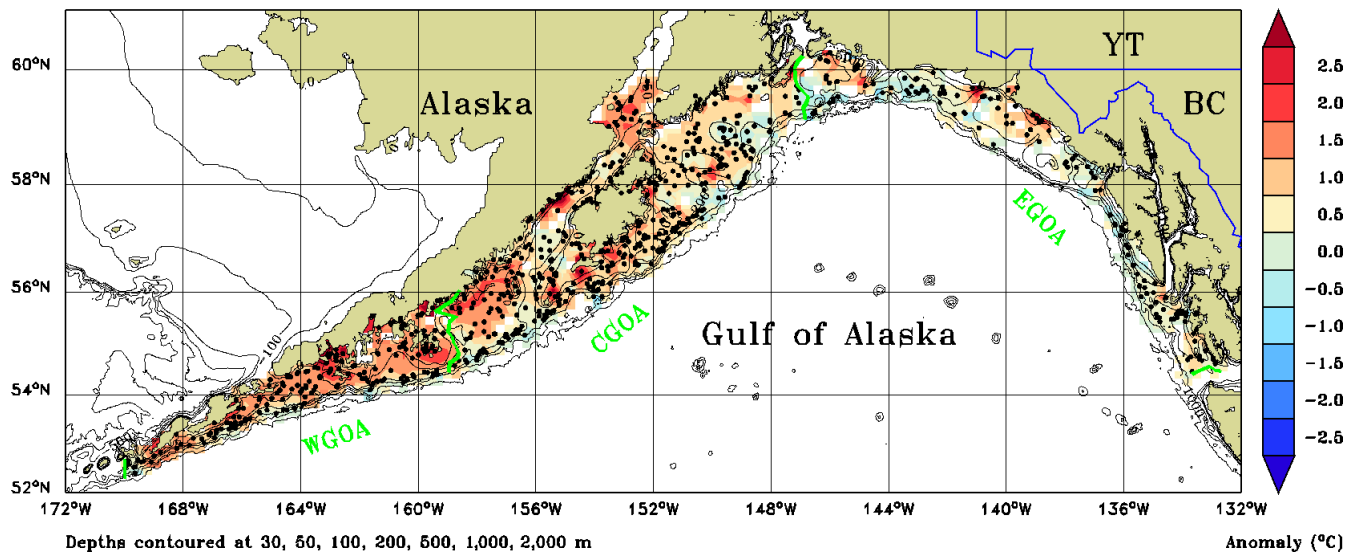


FIGURE 1 Bottom temperature anomalies (°C) in the Gulf of Alaska averaged over May–August in 2015. Anomalies are calculated relative to the 10-year mean. Regional boundaries for the western Gulf of Alaska (WGOA), central Gulf of Alaska (CGOA), and eastern Gulf of Alaska (EGOA) are shown as green lines [Colour figure can be viewed at wileyonlinelibrary.com]

a bottom trawl. Smoothness was judged by the lack of rugosity and the strength of the echo return which indicated that the seafloor was not composed of rock. Once located, a bottom trawl was conducted at the station using a Poly Nor'easter research net following established protocols to deploy, tow, and retrieve the net (Stauffer, 2004). Catches were sorted to species, weighed, and counted, and the area swept by the net was determined by multiplying the distance towed by the average width of the net opening as determined from acoustic sensors. The spatial density of each species was determined from the number of fish divided by the area fished (number per km²), hereafter referred to as catch per unit effort (CPUE; Figure 2). A random sample of commercially or ecologically important species, typically the majority of the fish species captured at each station, was measured to the nearest centimeter (fork length) from each trawl sample (von Szalay & Raring, 2016).

Temperature–depth observations were collected at every trawl survey station. Since 1993, a microbathymograph (MBT) has been attached to the headrope of each research trawl to measure the temperature from the surface to the operating depth of the trawl gear. The MBT was calibrated annually by the manufacturer. Initially, a Brancker XL200 MBT (Richard Brancker Research, Ltd., Kanata, ON, Canada) was used, and then in 2003, the Brancker MBT was replaced by the Sea-Bird (SBE-39) MBT (Sea-Bird Electronics, Inc., Bellevue, WA, USA). The mean bottom temperature for each tow was calculated as the average of all temperature observations during the time the net fished on the bottom. Several aspects of the survey have been modified over the time frame of analysis. Starting in 1996, the duration of each tow was reduced from 30 to 15 min. Noting these changes, we decided to use only data collected since 1996 to ensure consistency. A 10-year data set of bottom temperature, depth, and CPUE collected during ten research surveys (1996, 1999, 2001, 2003, 2005, 2007, 2009,

2011, 2013, and 2015) was used in this study. An analysis of the sampling in terms of depth, latitude, and longitude conducted by Li et al. (2018, in preparation) demonstrates that the trawl surveys are sufficiently consistent to describe the biennial variations in fish distributions.

Because the bottom trawl survey does not sample rocky or rugose habitats, there are potential biases that might be caused if fish move disproportionately between rugose and smooth seafloor habitats or pelagic habitats in response to temperature perturbations. Approximately 18% of the GOA habitats sampled during the bottom trawl survey have been determined to be untrawlable typically due to rocky and rugose seafloors. This finding is similar to those by Pirtle, Weber, Wilson, and Rooper (2015) and Baker, Palsson, Zimmermann, and Rooper (2018, in review) who used different approaches to characterize the rugosity of GOA seafloor habitats. The untrawlable habitat bias of the bottom trawl survey has been discussed by Cordue (2007) in terms of stock abundance estimation, and a number of species such as several rockfishes are denser than in rocky habitats and in surrounding smooth seafloor habitats (Jones et al., 2012; Williams, Rooper, & Towler, 2010). However, we chose species that do not necessarily have affinities for rocky habitats including three flatfish species and two gadids. As a rockfish, Pacific ocean perch are found in rocky habitats but are also frequently encountered in great abundance on smooth seafloors. The effect of untrawlable habitat on survey biomass estimates is an active area of research.

Habitat complexity within the GOA may afford opportunities for species to access a wide range of depths and temperatures without large spatial movements. That same habitat complexity constrains the availability of habitats to bottom trawl surveys (Rooper & Martin, 2012; Pirtle et al., 2015, and Baker et al., 2018, in review). While we recognize that it is possible that the six species we examined may differentially shift to untrawlable or pelagic habitats, the effect of

CGOA Bottom Trawl Survey, Pacific Cod CPUE, 2015

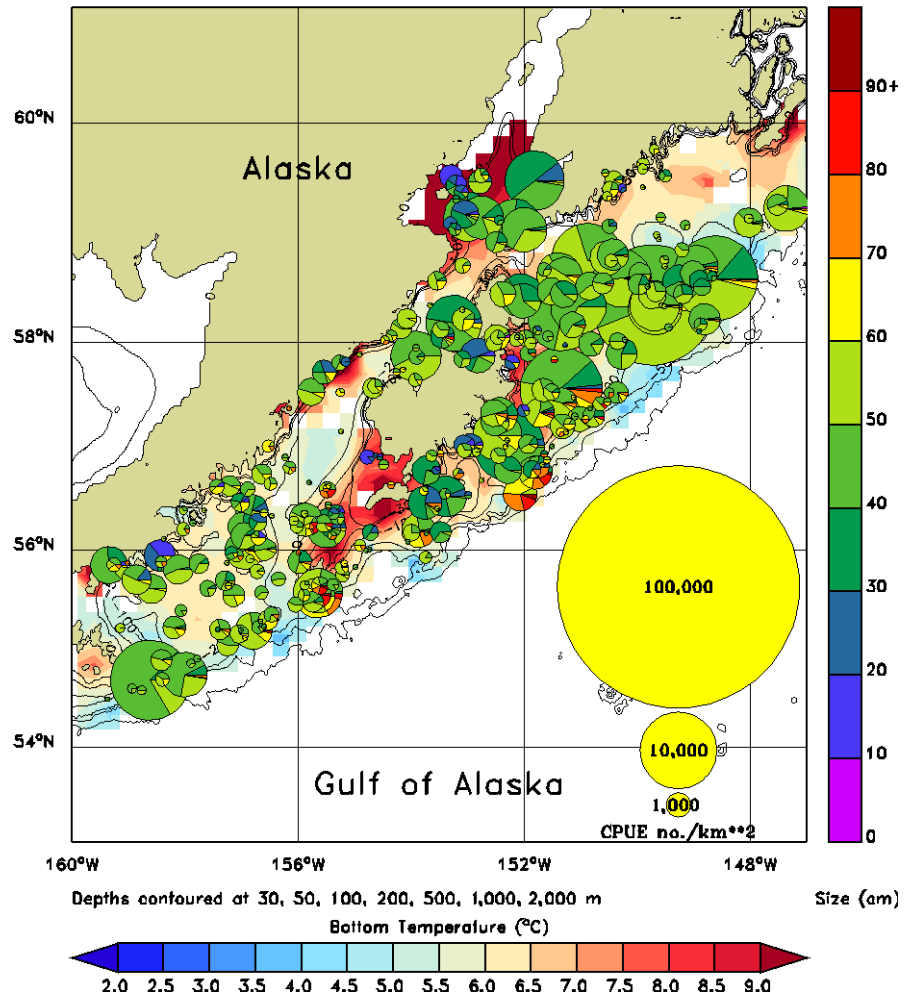


FIGURE 2 A map of Pacific cod catch per unit effort (CPUE; number per km²) in 2015 over the central Gulf of Alaska (CGOA) overlain with the temperature anomalies (scale at the bottom) from Figure 1. The pie charts illustrate the proportional distributions of CPUE from different size bins (color bar on the right), while the area indicates total CPUE [Colour figure can be viewed at wileyonlinelibrary.com]

these factors has not been examined by size groups and is therefore beyond the scope of this study.

2.2 | Annual means

Previous studies have assessed year-to-year variations in the habitat occupied by eastern Bering Sea groundfish, where habitat was defined by spatial envelopes of bottom temperature and depth (Baker & Hollowed, 2014; Barbeaux & Hollowed, 2018). This approach was applied to 10 years of survey data. Stratum areas vary between 773 km² and 15,403 km²; therefore, it was essential to take into account the stratum-area weighting in calculating the annual mean bottom temperature and depth available in a given survey year; that is,

$$\bar{T}_i = \frac{\sum_j \left(\frac{1}{n_{ij}} \sum_k T_{ijk} \right) \times A_j}{\sum_j A_j}, \quad (1)$$

$$\bar{D}_i = \frac{\sum_j \left(\frac{1}{n_{ij}} \sum_k D_{ijk} \right) \times A_j}{\sum_j A_j}, \quad (2)$$

where T_{ijk} and D_{ijk} are the bottom temperature and depth obtained from the i th year, j th stratum, and k th haul. A_j is the area of the j th stratum. For a given year, the available number of hauls within a

stratum is denoted by n_{ij} . The annual mean for each year was calculated and averaged to obtain the 10-year mean.

Similarly, the stratum-area-weighted annual mean centroid temperature and depth were calculated in a given survey year as

$$\bar{T}_{\text{centroid},i} = \frac{\sum_j \left(\frac{1}{n_{ij}} \sum_k \text{CPUE}_{ijk} \times T_{ijk} \right) \times A_j}{\sum_j \left(\frac{1}{n_{ij}} \sum_k \text{CPUE}_{ijk} \right) \times A_j}, \quad (3)$$

$$\bar{D}_{\text{centroid},i} = \frac{\sum_j \left(\frac{1}{n_{ij}} \sum_k \text{CPUE}_{ijk} \times D_{ijk} \right) \times A_j}{\sum_j \left(\frac{1}{n_{ij}} \sum_k \text{CPUE}_{ijk} \right) \times A_j}, \quad (4)$$

where CPUE_{ijk} is the CPUE from the i th year, j th stratum, and k th haul. Within a stratum, fish were binned by size into 10-cm bins (10-cm bin includes all fish 11–20 cm long; 20-cm bin includes 21–30 cm fish; etc) to account for ontogenetic differences, the rule-of-thumb being that larger fish are older fish.

2.3 | Probability density functions

For each survey year, we represented the habitat available to fish by computing a joint probability density function (PDF) of observed

bottom temperature and depth. As with the mean temperature calculated following Equation 1, these PDFs were computed including weighting by stratum area. The PDF, f_{habitat} , was constructed as the percent frequency of hauls, including hauls without catch, over $\Delta T = 1^\circ\text{C}$ and $\Delta D = 25\text{ m}$ intervals centered at bottom temperature t and depth d in a given survey year i as

$$f_{\text{habitat}_i}(t, d) = \frac{\sum_j \frac{1}{n_{ij}} N_{ij} \left(t - \frac{\Delta T}{2} \leq T < t + \frac{\Delta T}{2}, d - \frac{\Delta D}{2} \leq D < d + \frac{\Delta D}{2} \right) \times A_j}{\sum_j A_j} \times 100, \quad (5)$$

where N_{ij} is the available number of hauls that satisfy the temperature and depth criteria within a stratum. The total available number of hauls within a stratum is n_{ij} and A_j is the area of the j th stratum.

For a given survey year i , the distribution of fish abundance for species l can also be represented as a joint PDF (f_{fish}) of bottom temperature t and depth d as

$$f_{\text{fish}_{ij}}(t, d) = \frac{\sum_j \frac{1}{n_{ij}} \text{CPUE}_{ij,l} \left(t - \frac{\Delta T}{2} \leq T < t + \frac{\Delta T}{2}, d - \frac{\Delta D}{2} \leq D < d + \frac{\Delta D}{2} \right) \times A_j}{\sum_j \frac{1}{n_{ij}} \text{CPUE}_{ij,l} \times A_j} \times 100, \quad (6)$$

where $\text{CPUE}_{ij,l}$ is the total CPUE available over the 1°C (ΔT) temperature and 25 m (ΔD) depth intervals within the j th stratum in i th year for species l .

Probability density functions were calculated for each survey year to obtain the 10-year mean. The habitat and fish abundance PDF anomalies for a given survey year were then computed as the departures relative to the 10-year mean PDFs. To better illustrate the distributional changes in fish abundance, we removed the impact of habitat PDF anomaly by applying a linear regression to the fish abundance PDF anomaly:

$$\hat{f}'_{\text{fish}_{ij}}(t, d) = a \hat{f}'_{\text{habitat}_i}(t, d) + b, \quad (7)$$

where $\hat{f}'_{\text{habitat}_i}$ is the habitat PDF anomaly at the given year i , and $\hat{f}'_{\text{fish}_{ij}}$ is the fish abundance PDF anomaly at the given year i for species l . The coefficients of a and b were calculated based on the linear regression for fitted PDF anomaly $\hat{f}'_{\text{fish}_{ij}}$. With the influence of the habitat removed, the resulting residual fish abundance PDF, $e_{\text{fish}_{ij}}$, was calculated as

$$e_{\text{fish}_{ij}}(t, d) = \hat{f}'_{\text{fish}_{ij}}(t, d) - \hat{f}'_{\text{fish}_{ij}}(t, d). \quad (8)$$

3 | RESULTS

3.1 | Year-to-year variations of bottom temperatures

The 10-year mean bottom temperature in the WGOA (4.63°C) was colder than that observed in the CGOA (5.89°C ; Figure 3). In addition, the WGOA also exhibited larger year-to-year variations. These differences, however, can largely be attributed to the differences in survey months (timing) as the WGOA surveys were conducted earlier in the year (May and June) than those of the CGOA (June and July).

Winter and early spring temperatures in the WGOA are correlated with temperatures in the Bering Sea. During years with extensive ice, cold winds out of north often cross the Alaska Peninsula, resulting in particularly cold temperatures in the WGOA (Stabeno, Bond, & Salo, 2007). Data from a mooring in Pavlof Bay (100 m water depth) indicate that the water column in this region can remain well mixed into May. Conditions in the CGOA are different. This region is subject to significant horizontal advection associated with the counterclockwise circulation around the GOA shelf, and hence, temperatures are less influenced by the weather of the Bering Sea. In addition, there are locations of strong vertical mixing in the CGOA. In particular, water in Kennedy Entrance can be mixed to $>150\text{ m}$ because of the strong tides. This water is then advected down (southwestward) Shelikof Strait. Other regions of enhanced mixing include the troughs (e.g., Chiniak Trough) south of Kodiak Island (Stabeno et al., 2016). In other words, even in the stratified conditions of summer, the bottom temperatures of the CGOA are modified by the local mixing of warmer surface temperatures.

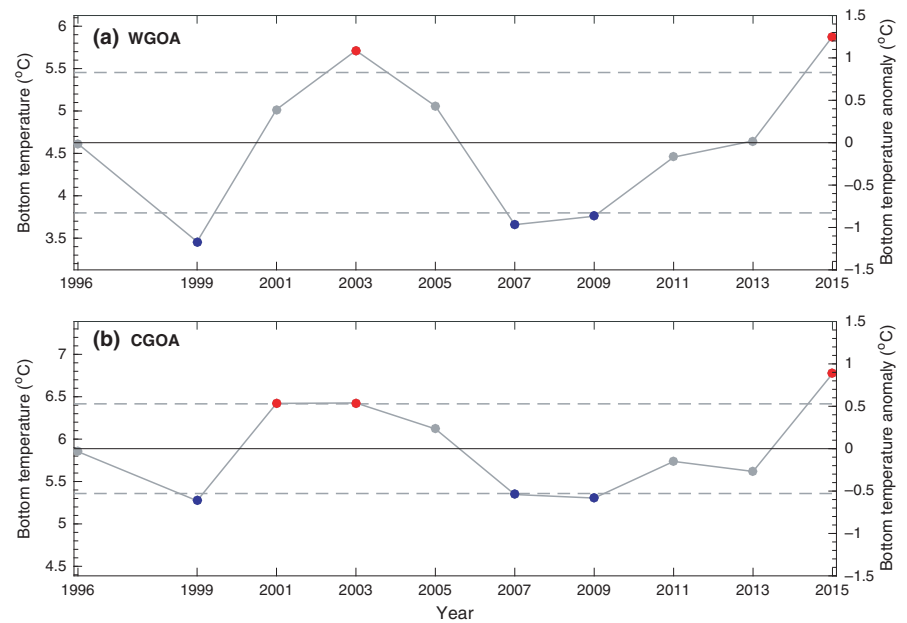
Each survey year was categorized as a warm, cold, or neutral year based on whether the annual mean bottom temperature was above ($>$ one standard deviation [1σ]), below ($<-1\sigma$), or within $\pm 1\sigma$ of the 10-year mean bottom temperature. There were two warm years (2003 and 2015), three cold years (1999, 2007, and 2009), and five neutral years (1996, 2001, 2005, 2011, and 2013) in the WGOA. In the CGOA, there were three warm years (2001, 2003, and 2015), three cold years (1999, 2007, and 2009), and four neutral years (1996, 2005, 2011, and 2013).

"The Blob" year, 2015, was the warmest among the 10 survey years across the entire GOA (Figure 3 and Table 1). In 2015, the WGOA had a mean bottom temperature of 5.88°C , which is 1.25°C warmer than the 10-year mean (Figure 3a). In 2015, the CGOA had a mean bottom temperature of 6.77°C which was 0.88°C warmer than the 10-year mean and 0.34°C warmer than the second warmest year in 2003 (Figure 3b). The year 2003 was the second warmest year in both the WGOA and CGOA, corresponding with an El Niño event (McPhaden, 2004). In 1999, a La Niña year, the WGOA and CGOA were the coldest with a bottom temperature anomaly of -1.17°C in the WGOA and -0.61°C in the CGOA, respectively (Whitney & Welch, 2002).

3.2 | Probability density functions of habitat and fish abundance

Probability density functions of the overall survey bottom temperature and depth in 2015 (Figure 4a) and the 10-year mean (Figure 4b) in the CGOA showed a bimodal distribution with one maximum located near 80 m representing inner-shelf trawls and another near 180 m representing the average depth of outer-shelf trawls. The negligible difference (0.45 m) between the 2015 and the 10-year mean bottom depths implies consistency in survey depth (horizontal dashed lines in Figure 4a,b). Compared with the 10-year mean, 2015 had a narrower bottom temperature range. Waters were warmer at all depths in 2015 with many more warm-temperature and fewer

FIGURE 3 Annual mean stratum-area-weighted bottom temperatures (left axis) and bottom temperature anomalies (right axis) averaged over the (a) western Gulf of Alaska (WGOA) and (b) central Gulf of Alaska (CGOA) from 10 bottom trawl survey years (1996, 1999, 2001, 2003, 2005, 2007, 2009, 2011, 2013, and 2015). The horizontal black lines denote the 10-year mean. The gray dashed lines are ± 1 standard deviation (σ) of the mean. Warm years ($T_{\text{anomaly}} > 1\sigma$), cold years ($T_{\text{anomaly}} < -1\sigma$), and neutral years ($-1\sigma \leq T_{\text{anomaly}} \leq 1\sigma$) are shown in red, blue, and gray, respectively [Colour figure can be viewed at wileyonlinelibrary.com]



cold-temperature hauls (Figure 4c). Averaged over all surveyed depths, waters in 2015 were 0.88°C warmer than the 10-year mean (Figure 3b and Table 1).

The Pacific cod 50-cm-size interval exhibited the most distinct distributional shift and therefore was used as an example to illustrate our key findings (Figure 4d–g). The PDFs of Pacific cod of other sizes are available as Supporting Information (Figures S1–S6). In recent years (1996–2015), the majority of 50-cm Pacific cod were found in a bottom temperature range of 4.5–6°C within a bottom depth range of 80–105 m (Figure 4e). The 10-year mean centroid temperature and depth were 5.8°C and 109.4 m, respectively. The cool habitat with temperatures of 4.5–6°C at depths of 80–105 m was absent in 2015 (Figure 4d). The minimum available temperature at depths of 80–105 m was 6°C in 2015. Instead of one population peak, there were three preferred cod population peaks with warmer bottom temperatures in 2015. The most prominent peak, with a

maximum probability of 17%, was found near the bottom temperature of 6°C and a much deeper depth of 180 m. The second peak was located near 7°C at the depth of 130 m with a maximum probability of 12%. The third one was at 80 m, the same depth as the 10-year mean, but with a warmer temperature of 8°C; the maximum probability was 8.4%. As a result, the anomaly field of 50-cm Pacific cod abundance in 2015 showed distinct distributional changes in both temperature and depth (Figure 4f). On the temperature axis, dense concentrations of cod were found in warmer waters than their preferred range of 4.5–6°C due to the absence of cooler habitat in 2015. On the depth axis, dense concentrations of fish were found around depths of 180, 130, and 80 m and less dense concentrations were observed near the 10-year mean peak of 80 m. Compared with the 10-year mean, the mean centroid temperature increased by 0.91°C and the mean centroid depth deepened by 26 m in 2015, as shown by the arrow in Figure 4f.

The thermal-depth habitat influence on the PDF anomaly of Pacific cod abundance was negligible for juveniles (10 cm), but significant for larger cod, explaining more than half of the variance found in the PDF anomaly of 50-cm Pacific cod (Table 2). These findings suggest that small cod are responding to drivers other than temperature, such as those governing the foraging arena (Walters & Kitchell, 2001).

After removal of the habitat influence, the residual 50-cm Pacific cod clearly showed a negative PDF anomaly near 80 m and 6°C, where the 10-year mean PDF of fish abundance peaked (Figure 4g). Three positive anomaly residuals were located near 80, 130, and 150 m, with the latter two accounting for the majority of the population movement. This implied that in 2015 more 50-cm Pacific cod were caught in deeper waters in response to the warmer than normal habitat. Pacific cod of other sizes exhibited similar responses in 2015 (Supporting Information Figures S1–S6).

Similar to Pacific cod, more 20-cm arrowtooth flounder were caught in deeper waters in 2015 (Figure 5d–g). In the 10-year

TABLE 1 Annual mean bottom temperature (°C) and bottom temperature anomaly (°C) over the western Gulf of Alaska (WGOA) and central Gulf of Alaska (CGOA)

Year	WGOA		CGOA	
	T	T _{anomaly}	T	T _{anomaly}
1996	4.61	-0.01	5.85	-0.03
1999	3.46	-1.17	5.27	-0.61
2001	5.02	0.39	6.42	0.53
2003	5.71	1.09	6.43	0.54
2005	5.06	0.43	6.12	0.23
2007	3.66	-0.97	5.35	-0.54
2009	3.76	-0.87	5.30	-0.58
2011	4.46	-0.17	5.74	-0.15
2013	4.65	0.02	5.62	-0.27
2015	5.88	1.25	6.77	0.88

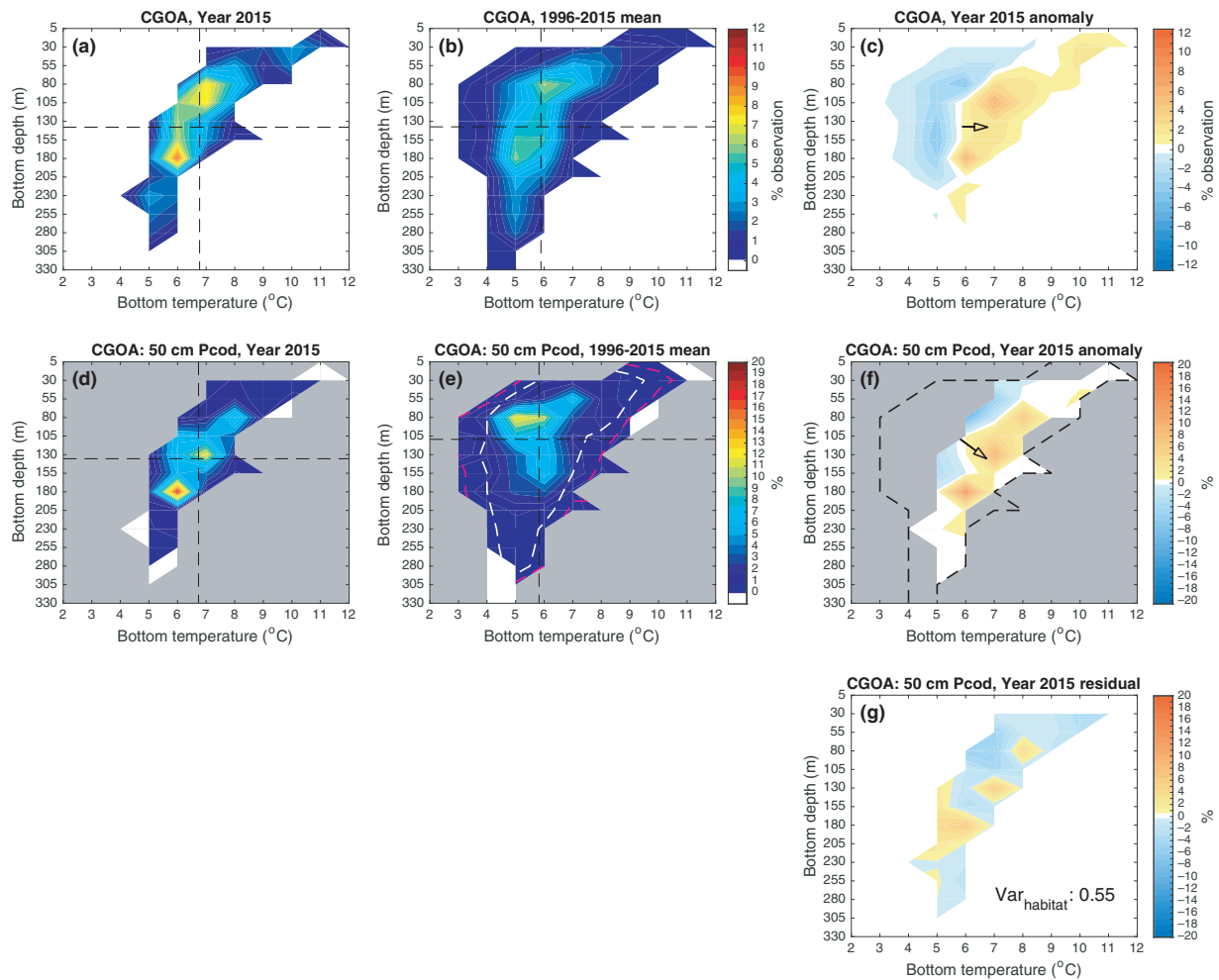


FIGURE 4 Joint probability density functions (PDFs) of (a) habitat defined as bottom temperature and bottom depth in 2015, (b) 10-year mean habitat, and (c) habitat anomaly from the 10-year mean in 2015 over the central Gulf of Alaska (CGOA). The vertical and horizontal dashed lines denote the stratum-weighted mean bottom temperature and depth. White areas represent no samples in (a–c). In (c), the overlaid arrow illustrates the direction of change in mean bottom temperature and depth. The tail of the arrow begins at the 10-year mean bottom temperature and depth and the head of the arrow ends at the 2015 bottom temperature and depth. (d–f) are the same as (a–c), but for PDFs weighted by the catch per unit effort (CPUE) of 50-cm (51–60 cm) Pacific cod abundance. In (e), the magenta and white dashed contours outline the habitat available for more than 2 and 5 out of the 10 years, respectively. In (f), the dashed outline bounds the habitat available in all years. The gray shading indicates no available habitat. The white areas represent zero fish catch. (g) is the residual PDF of 50-cm Pacific cod abundance after removing the impact of habitat. In (f), the overlaid arrow illustrates the direction of change in mean centroid bottom temperature and depth. The tail of the arrow begins at the 10-year mean centroid bottom temperature and depth, and the head of the arrow ends at the 2015 mean centroid bottom temperature and depth [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Variance explained by habitat changes in 2015 over the central Gulf of Alaska (CGOA)

Species	Size (cm)						
	10 (11–20)	20 (21–30)	30 (31–40)	40 (41–50) ^a	50 (51–60) ^b	60 (61–70) ^c	>70
Pacific cod	0.02 (61)	0.1 (195)	0.18 (888)	0.42 (2,381)	0.55 (1,896)	0.47 (305)	0.31 (185)
Arrowtooth flounder	0.24 (297)	0.52 (7,863)	0.6 (8,432)	0.56 (7,482)	0.55 (5,229)	0.38 (447)	0.1 (41)
Walleye pollock	0.1 (1,327)	0.09 (369)	0.01 (1,660)	0.21 (2,602)	0.14 (3,751)	0.1 (339)	N/A
Pacific ocean perch	0.1 (269)	0.02 (1,306)	0 (9,671)	0.01 (2,862)	N/A	N/A	N/A
Northern rock sole	0.18 (302)	0.18 (1,010)	0.16 (734)	0.16 (259)	N/A	N/A	N/A
Southern rock sole	0.12 (109)	0.19 (1,034)	0.16 (1,419)	0.27 (1,539)	0.21 (95)	N/A	N/A

Notes. Number of individuals caught in 2015 over the CGOA is shown in the parenthesis.

^a>40 cm for Pacific ocean perch and northern rock sole. ^b>50 cm for southern rock sole. ^c>60 cm for walleye pollock.

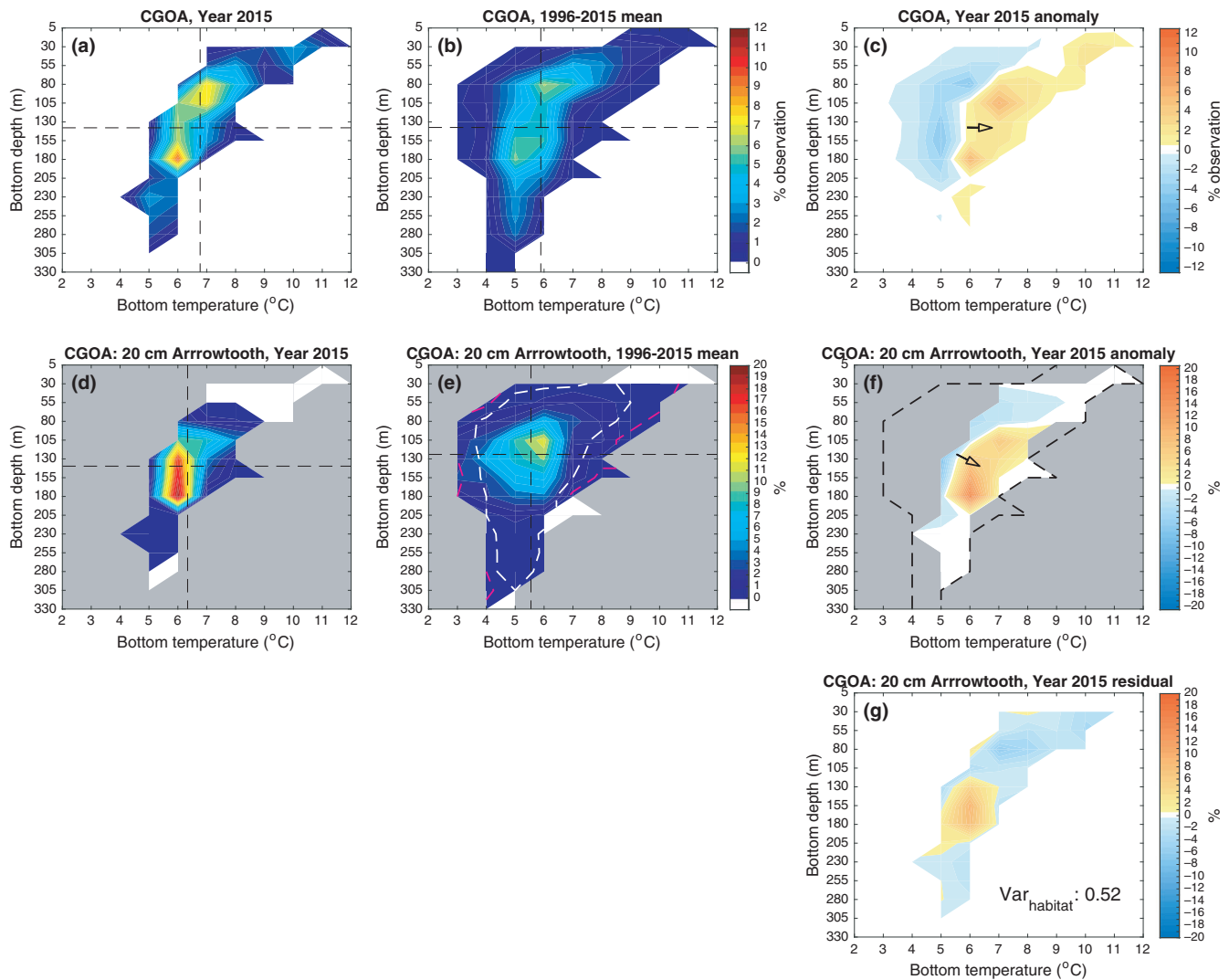


FIGURE 5 Same as Figure 4, but for the 20-cm (21–30 cm) arrowtooth flounder [Colour figure can be viewed at wileyonlinelibrary.com]

average, arrowtooth flounder density peaked in bottom temperatures ranging from 5.5 to 6°C and bottom depths ranging between 105 and 130 m, with the mean centroid temperature of 5.55°C and centroid depth of 124.01 m, respectively (Figure 5e). In 2015, the arrowtooth flounder shifted to warmer (~6°C) and deeper (130–190 m) waters with the mean centroid temperature of 6.34°C and centroid depth of 139.68 m, which was 0.79°C warmer and 15.67 m deeper than the 10-year means (Figure 5d). After removal of the habitat influence, which accounted for 52% of the variance found in the anomaly PDF of fish abundance (Figure 5f and Table 2), the residual highlighted a positive anomaly located at depths of 130–190 m and a negative anomaly at shallower depths with a peak depth of around 80 m (Figure 5g). This indicated that more 20-cm arrowtooth flounder were caught at deeper waters (130–190 m) and fewer were caught at shallower waters (<130 m), in response to the anomalously warm ocean waters in 2015. Such a population distributional shift to deeper waters was also observed in other sizes of arrowtooth flounder (Supporting Information Figures S7–S12).

In contrast to Pacific cod and arrowtooth flounder, the other four species had weaker habitat responses to the anomalous ocean conditions associated with the marine heatwave of 2014–2016 (Table 2). Both walleye pollock and Pacific ocean perch showed ontogenetic variations in response to warmer temperatures in 2015. Small pollock (10–30 cm) shifted to on-shelf shallower waters (Supporting Information Figures S13–S15), while larger pollock (40–60 cm) shifted to deeper waters (Supporting Information Figures S16–S18). Similarly, 10-cm Pacific ocean perch shifted to shallower waters (Supporting Information Figure S19), while the 40-cm Pacific ocean perch shifted to deeper waters in 2015 (Supporting Information Figure S22). The PDF anomaly of 20-cm Pacific ocean perch showed two positive anomalies around 80 and 180 m with a negative anomaly in the middle around the 10-year mean population peak of 155 m, indicating some of the 20-cm Pacific ocean perch shifted from the 10-year mean to shallower waters while the rest shifted to deeper waters (Supporting Information Figure S20). Overall, 20-cm Pacific ocean perch were

caught in shallower waters as indicated by the reduced centroid depth in 2015 compared with the 10-year mean (Supporting Information Figure S20f). The 30-cm Pacific ocean perch exhibited an opposite PDF anomaly to the 20-cm Pacific ocean perch, with a positive anomaly around the 10-year mean habitat depth of 180 m and two negative anomalies peaked around 130 and 205 m (Supporting Information Figure S21). Therefore, 30-cm Pacific ocean perch tended to cluster to their 10-year mean centroid depth in response to warmer habitat. Both northern and southern rock soles showed relatively smaller distributional changes in response to the warmer habitat in 2015 (Supporting Information Figures S23–S31).

3.3 | Changes in centroid depths in response to habitat temperature changes

In 2015, warmer than normal waters were found at all depths where the six species of all sizes resided (Figure 6). An ontogenetic shift, with larger sizes found deeper, was observed in Pacific cod, arrowtooth flounder, Pacific ocean perch, and walleye pollock (Figure 6a–d). Pacific cod of all sizes (10–70 cm) showed a distributional shift to deeper waters in 2015 (Figure 6a). Adult cod (>30 cm) had greater changes in centroid depth than younger cod. Similarly, the centroid depths of 20- to 60-cm arrowtooth flounder deepened in 2015 compared with the 10-year means (Figure 6b). Although statistically insignificant, the 10-cm arrowtooth flounder showed a negligible change in centroid depth, while 70-cm arrowtooth flounder tended to be found slightly deeper. Larger walleye pollock (>30 cm) showed a deeper shift, while smaller ones showed a shallower shift (Figure 6c). Small-sized Pacific ocean perch (10 and 20 cm) exhibited a significant distributional shift to shallower waters, while larger ones (40 cm) tended to be found in deeper waters (Figure 6d). The 20- and 30-cm northern rock sole showed a slight deeper shift, while the larger 40-cm ones showed an opposite slight shift toward shallower waters (Figure 6e). The 10- and 20-cm southern rock sole were observed to have distributional shifts to deeper waters (Figure 6f). In summary, the six groundfish species exhibited various responses to the anomalously warm ocean conditions in 2015. Two piscivorous species (Pacific cod and arrowtooth flounder) showed distributional shifts to deeper waters. Pelagic planktivores (walleye pollock and Pacific ocean perch) of larger size moved deeper, while smaller ones moved shallower. Small-sized benthivores (northern and southern rock soles) shifted their distributions to greater depths.

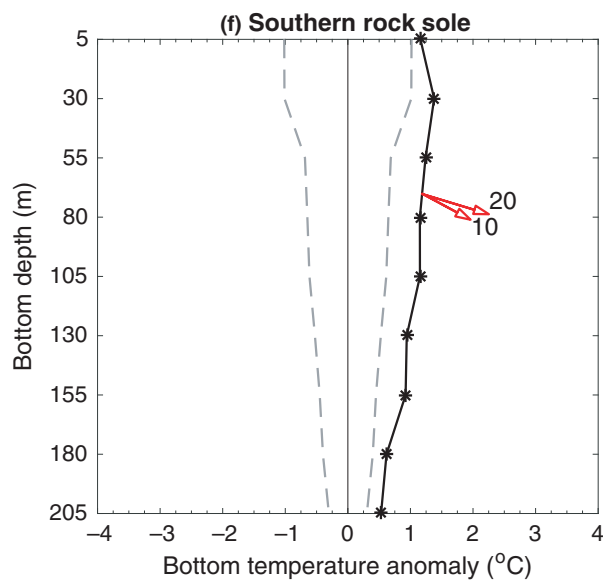
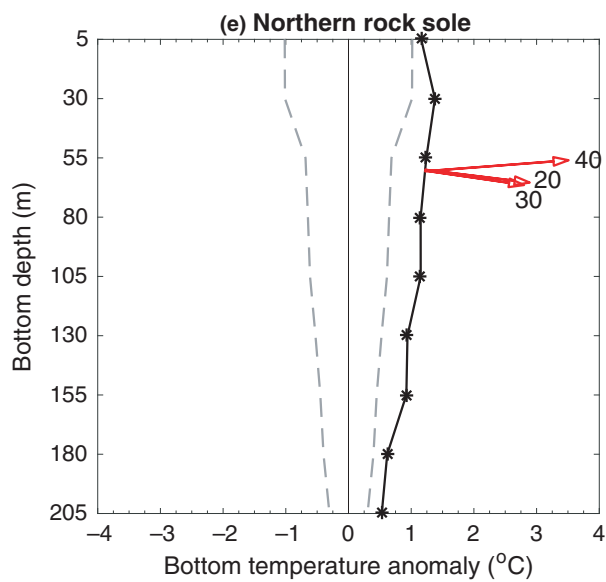
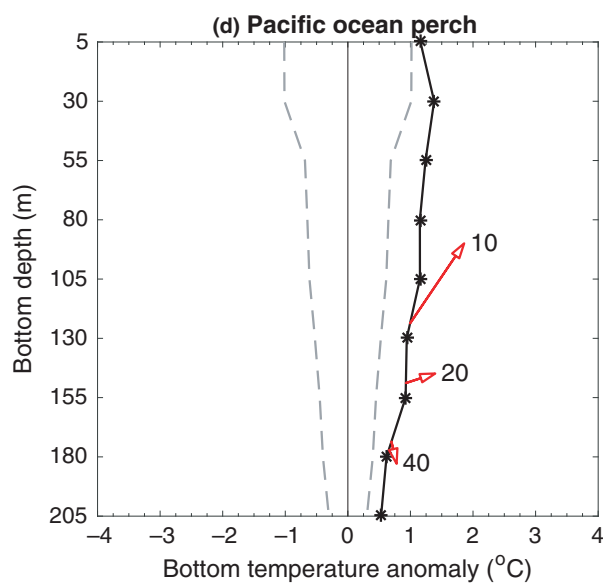
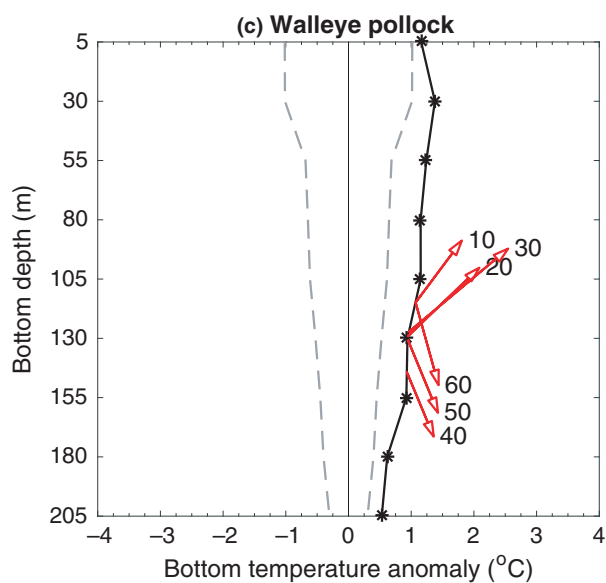
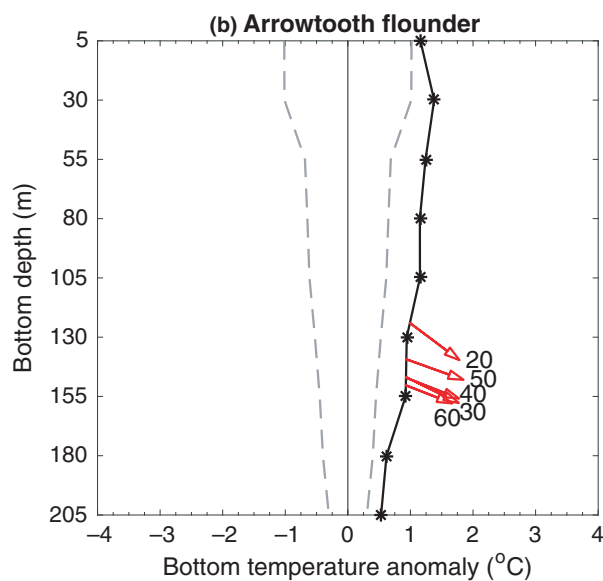
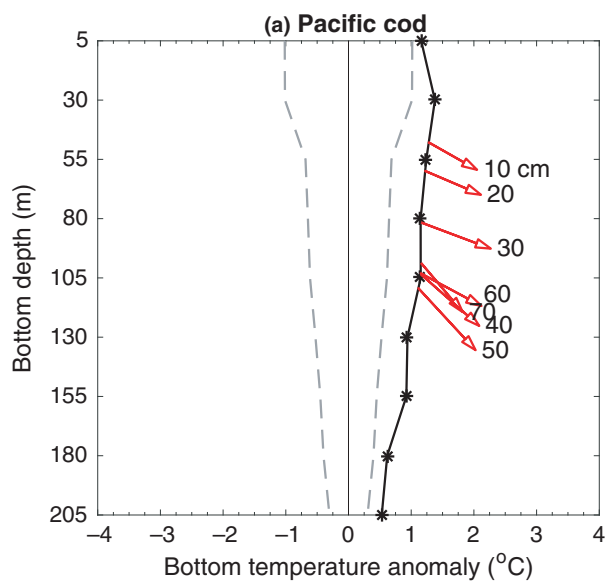
In 2003, the second warmest year of the 10 survey years, waters were significantly warmer than average between 30 and ~150 m (but to a lesser extent than was observed in 2015) and were near normal above 30 m and below 150 m (Figure 7). Waters were significantly warmer than average in 2003 for the depths where Pacific cod resided. Pacific cod of all sizes showed distributional shifts to deeper waters except for juveniles (10 cm; Figure 7a). Arrowtooth flounder resided at deeper depths than Pacific cod over the ten survey years (Figure 7b). Thus, only the juveniles (10 cm) were seemingly affected by the warmer habitat in terms of their centroid depth. As in 2015, the 10- and 20-cm pollock shifted to shallower waters (Figure 7c). Northern rock sole at sizes of 10, 20, and 40 cm were in shallower waters (Figure 7e). Southern rock sole at sizes of 20 and 50 cm were in deeper waters (Figure 7f).

Although the annual mean bottom temperature of 2001 was significantly warmer than the 10-year mean (Figure 3), the bottom temperatures were near normal at the habitat depths of six groundfish species except for 50-cm pollock and 30- and 40-cm Pacific ocean perch (Supporting Information Figure S32). The pollock at 50 cm had a greater centroid depth, while the 30- and 40-cm Pacific ocean perch showed an upward shift in centroid depth.

It is interesting to compare the distributions of groundfish during colder conditions with those during warmer conditions as described above. The La Niña year of 1999 was the coldest year among the 10 survey years, during which it was significantly colder than the 10-year mean from the surface down to a depth of 105 m, with near normal temperatures below (Figure 8). Therefore, the bottom temperature anomalies in 1999 were neutral at the water depths where arrowtooth flounder, walleye pollock, and Pacific ocean perch normally reside (Figure 8b–d). In response to the colder than normal habitat, Pacific cod showed distributional shifts to shallower waters except for the 40-cm-size fish, which moved slightly deeper. This might be explained by the nearly neutral temperature anomaly at which 40-cm Pacific cod resided (Figure 8a). The 10- and 20-cm northern rock sole and 10-cm southern rock sole moved to shallower waters relative to the 10-year mean (Figure 8e,f).

The year 2009 represented the second coldest survey year with an annual mean bottom temperature of only 0.03°C warmer than the coldest year of 1999 (Figure 3). During 2009, the bottom temperatures were neutral at depths of 30–55 m where 10-cm Pacific cod and 10-cm northern rock sole resided (Figure 9), but were significantly colder at other depths (Figure 9). Pacific cod of all sizes showed a shift to shallower centroid depths in response to colder

FIGURE 6 Changes in the centroid temperatures and depths of (a) Pacific cod, (b) arrowtooth flounder, (c) walleye pollock, (d) Pacific ocean perch, (e) northern rock sole, and (f) southern rock sole, in response to habitat bottom temperature anomalies in 2015 over the central Gulf of Alaska (CGOA). The vertical profiles of habitat bottom temperature anomaly (solid lines) were obtained by averaging all available bottom temperature anomalies within a 25-m layer. The dashed lines represent $\pm 1\sigma$ of the bottom temperature anomalies. The anomaly was calculated relative to the 10-year mean. The overlaid arrows illustrate the direction of changes in the mean centroid temperature and depth as shown in Figures 4f and 5f for difference size bins. In the vertical, the tail of the arrow begins at the 10-year mean centroid depth, and the head of the arrow ends at the annual mean centroid depth in 2015. The horizontal component of the arrow denotes the change in the mean centroid temperature in 2015, relative to the 10-year mean centroid temperature. The arrows were plotted only if the change in centroid depth is statistically significant at the 95% level based on the two-sided Student's *t* test [Colour figure can be viewed at wileyonlinelibrary.com]



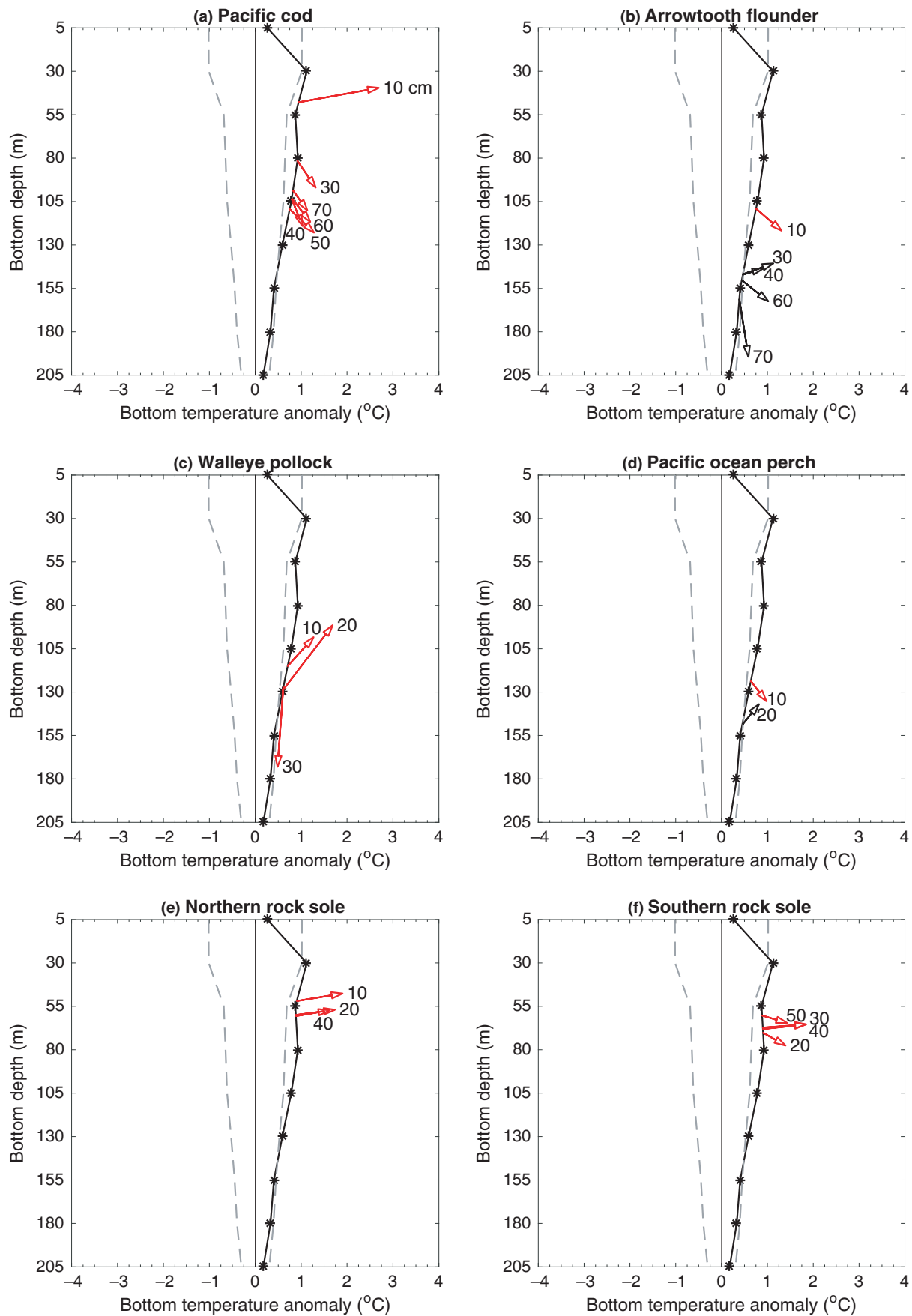


FIGURE 7 Same as Figure 6, but for 2003, the second warmest year. The overlaid arrows were plotted in red when the bottom temperature anomaly at the 10-year mean centroid depth was significantly larger than 1σ and in black if less than or equal to that [Colour figure can be viewed at wileyonlinelibrary.com]

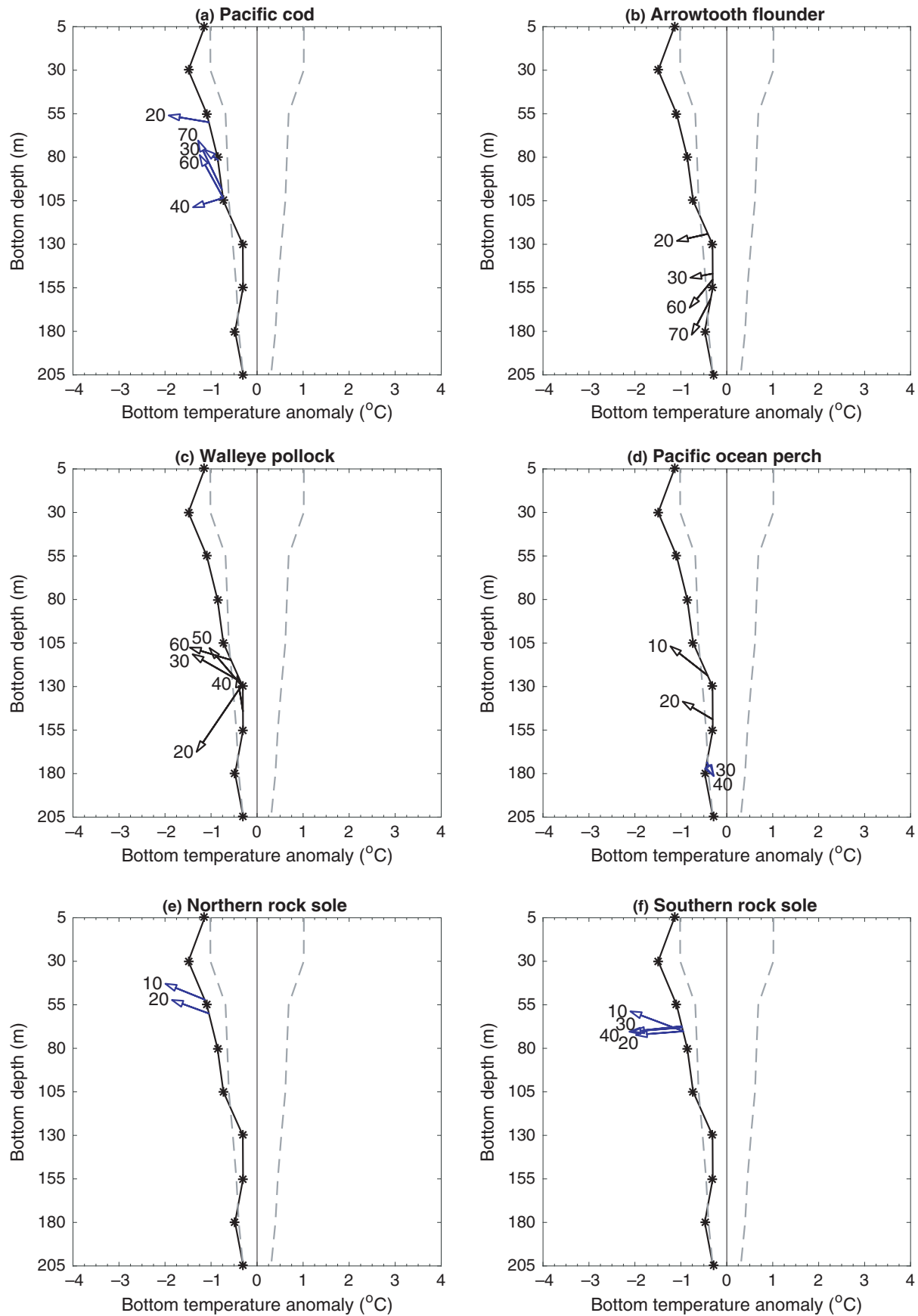


FIGURE 8 Same as Figure 6, but for 1999, the coldest year. The overlaid arrows were plotted in blue when the bottom temperature anomaly at the 10-year mean centroid depth was significantly smaller than -1σ and in black if less than or equal to that [Colour figure can be viewed at wileyonlinelibrary.com]

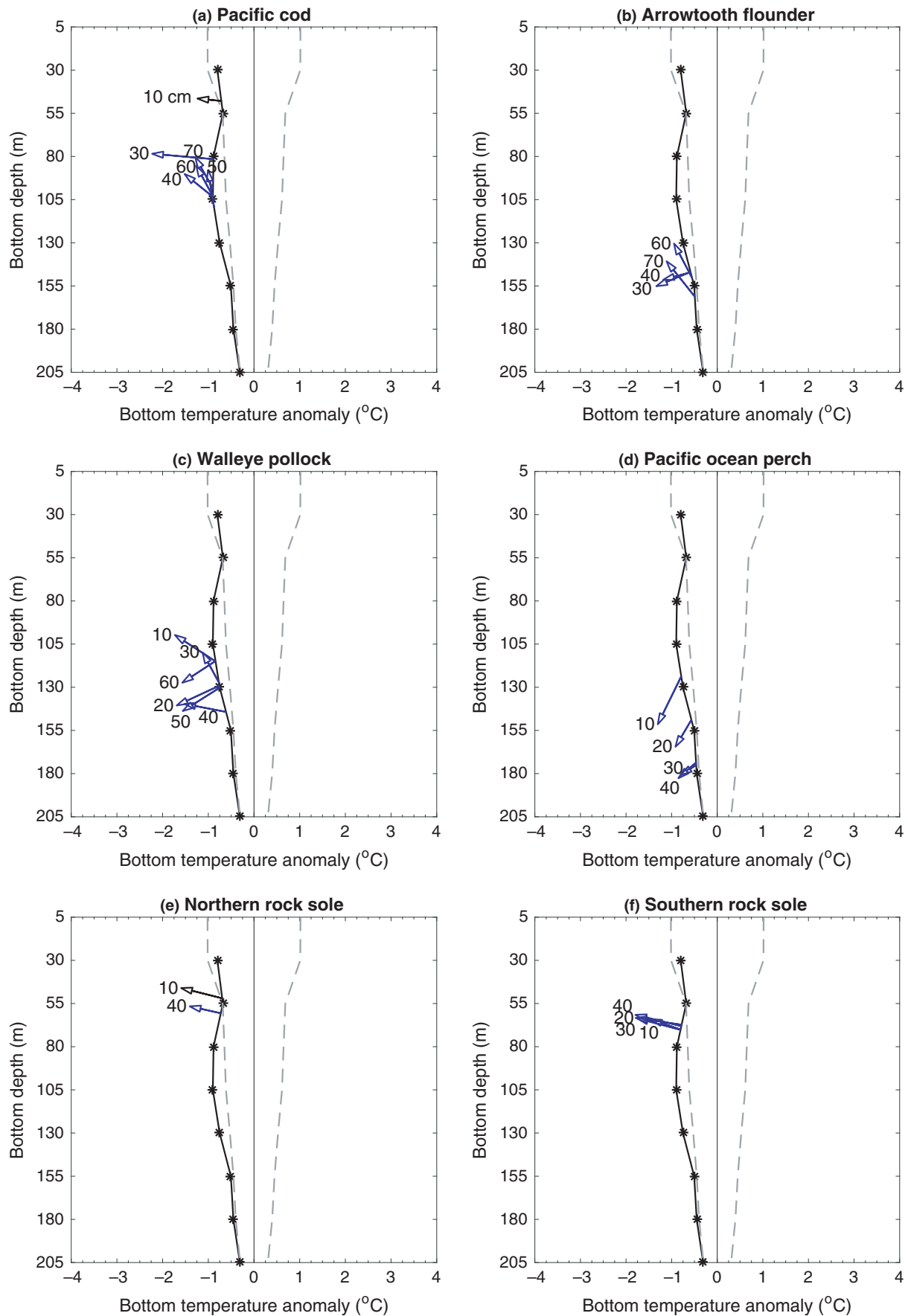


FIGURE 9 Same as Figure 8, but for 2009, the second coldest year [Colour figure can be viewed at wileyonlinelibrary.com]

habitat (Figure 9a). The 60- and 70-cm arrowtooth flounder also shifted to shallower waters, while the 30- and 40-cm individuals were deeper (Figure 9b). The 10-, 30-, and 40-cm pollock were in shallower waters, and the 20-, 50-, and 60-cm pollock were in deeper waters (Figure 9c). All sizes of Pacific ocean perch showed distributional shifts to greater depths (Figure 9d). In contrast, all sizes of northern and southern rock sizes showed distributional shifts to lesser depths (Figure 9e,f).

In 2007, the bottom temperatures were near normal except at the habitat depths of arrowtooth flounder, Pacific ocean perch, and 20- to 50-cm walleye pollock (Supporting Information Figure S33). As in 2009, smaller arrowtooth flounder (20–40 cm) moved deeper while larger sizes (50–70 cm) moved shallower. All sizes of Pacific ocean perch showed distributional shifts to greater depths. The 20- and 50-cm pollock had shallower centroid depths.

The distributional shifts in groundfish centroid depths as a function of bottom temperature anomaly (considering the depth where each species and size interval normally reside) over the 10 survey years are summarized as scatter plots in Figure 10. In general, Pacific cod had a positive change in centroid depth (moved deeper) in response to warmer waters and a negative change in centroid depth (moved shallower) in colder waters (Figure 10a). Arrowtooth flounder of all sizes shifted deeper in warmer conditions. In response to colder conditions, large-sized individuals (>40 cm) tended to be in shallower waters while small ones shifted to deeper waters (Figure 10b). In response to warmer habitats, smaller sizes of pollock (10 and 20 cm) shifted to shallower waters while larger ones (>30 cm) moved deeper (Figure 10c). Pacific ocean perch showed an opposite response to colder habitats, compared to Pacific cod and arrowtooth flounder, shifting deeper in colder waters. Their response to warmer waters was ambiguous with some sizes moving deeper and others moving shallower (Figure 10d). The changes in centroid depth in response to habitat changes from both northern and southern rock soles were smaller in magnitude relative to the other four species. Northern rock sole tended to be found shallower in colder waters (Figure 10e). Southern rock sole did not exhibit a clear response to habitat changes (Figure 10f).

We also performed the same analysis to WGOA, but no discernible responses were found to habitat temperature changes (Figure 11). Further research is needed to understand such regional differences in groundfish response to habitat temperature changes. Li et al., 2018 (in preparation) discussed the influence of sub-regional differences in oceanography and topography on fish distributional responses to habitat temperature changes across the GOA as well as west coast of Canada and United States.

4 | SUMMARY AND DISCUSSION

Thermal anomalies near the ocean's surface do not necessarily correspond with those at depth. In other words, while gulfwide sea surface temperature (SST) is often used to characterize oceanic thermal properties, it can be misleading as an index of the distribution of

suitable habitat for fish within a region. For example, the Climate Forecast System Reanalysis (CFSR; Saha et al., 2010) SST averaged over the survey months from May through August showed strongly positive anomalies across the entire GOA in 2015 (Supporting Information Figure S34). The vertical extent of warming, however, is not spatially homogeneous, as indicated in bottom temperature, with extensive warming and scattered cooling evident over the GOA (Figure 1).

Ocean reanalysis products for estimating temperatures at depth are useful for specifying broad-scale distributions and variability of ocean conditions, especially since 2005 when vertical profile information from the Argo project became increasingly available for assimilation. However, Argo floats were limited over shelf regions. Therefore, it was highly beneficial to use in situ temperature–depth observations compared with model-based estimates of deeper water column temperatures, which may not adequately match ambient conditions and the subtle responses of fish to temperatures and depth. In this study, we have taken advantage of the observations from the bottom trawl survey to relate fish distributions to actual observed temperatures in their habitats, recognizing that variations in the dates of data collection introduce uncertainties in comparisons among years.

The long-term AFSC bottom trawl survey allowed us to investigate the distributional shifts of groundfish in response to habitat temperature changes in the CGOA, especially the response to the anomalously warm ocean conditions in 2015. Previous analyses of this sort commonly used indices such as centroids of distribution or center of gravity (Pinsky et al., 2013; Spencer, 2008). Our method yielded a more complete quantification of relative contributions of year-to-year variations in the availability of temperature–depth habitat surfaces while taking into account size-structured movements. Our results were consistent with previous studies on Bering Sea groundfish, which concluded that groundfish exhibit complex distributional responses to changes in ocean temperatures that were related to species-specific ontogeny (Barbeaux & Hollowed, 2018) and species-specific spatial partitioning within temperature–depth habitat surfaces (Baker & Hollowed, 2014; Kotwicki & Lauth, 2013). Failing to account for these species-specific behavioral responses could lead to misleading conclusions regarding the role of climate forcing on juvenile and adult fish distributions, particularly in species that exhibit sporadic strings of recruitment events where the spatial distribution of the population would be dominated by a small number of size groups.

We are cautious about drawing conclusions about how the six species examined here may have shifted their geographic location because we focused on the thermal and depth components of habitat but did not explicitly map pelagic prey distributions. While cooler bottom temperatures occurred in the outer shelf (Figures 1 and 2), they also occurred in the gullies and troughs that incise the GOA. Topographically controlled flow through these troughs creates fronts that serve to partition juvenile pollock and capelin (*Mallotus villosus*; Hollowed, Wilson, Stabeno, & Salo, 2007; Lagerloef, 1983). Therefore, species such as Pacific cod and arrowtooth flounder may not

FIGURE 10 Vertical distributional shifts of (a) Pacific cod, (b) arrowtooth flounder, (c) walleye pollock, (d) Pacific ocean perch, (e) northern rock sole, and (f) southern rock sole, in response to environmental temperatures in the central Gulf of Alaska (CGOA) based on the 10-year bottom trawl survey. The temperature anomalies warmer than one standard deviation ($+1\sigma$) are colored in red, and the temperature anomalies colder than -1σ are shown in blue. All the neutral temperatures, which fall within the range of $\pm 1\sigma$, are shown in black. The ordinate shows the changes in CPUE-weighted depth. The positive (negative) values indicate a deeper (shallower) centroid depth, compared to the 10-year mean. The sizes of dots represent lengths of cod ranging from 0–10 cm to 70+ cm. Only those values of vertical change in centroid depth which are statistically significant at the 95% level based on the two-sided Student's *t* test are shown [Colour figure can be viewed at wileyonlinelibrary.com]

have had to move very far geographically to experience deeper and cooler waters with potentially dense prey resources during warmer years.

Our results revealed similar responses of two piscivorous groundfish to ocean warming, but differing responses to colder ocean conditions. In general, Pacific cod shifted deeper during warmer years and shallower in colder years. Arrowtooth flounder also moved deeper in warmer years. However, in colder years, larger-sized arrowtooth flounder (>40 cm) shifted shallower, while smaller-sized ones shifted deeper. For larger-sized arrowtooth flounder, walleye pollock were the primary prey in their diet (Knoth & Foy, 2008; personal communication with Dr. Kerim Aydin). The shallower shift in large arrowtooth flounder is consistent with the shallower shift in 10-cm walleye pollock in colder years. The different responses of small and large arrowtooth flounder in the CGOA suggest that prey availability may be a key driver for habitat selection for this species. These findings illustrate the complex role of temperature in regulation of predatory species.

Shifts in larger-sized piscivorous species were likely due to balancing the negative impacts of increased metabolic stress imposed by warmer temperatures and the negative impacts of cooler temperatures on attack speed of predators and escape speed of prey (Öhlund, Hedström, Norman, Hein, & Englund, 2015) as well as temperature effects on prey availability. The different regional responses may also be related to the combined effects of temperature and spatial distributions of prey. The 2014–2016 year classes of walleye pollock were all below average (Dorn et al., 2017). Juvenile walleye pollock are typically found in shallow-water inshore of the mid-trough fronts in Chiniak and Barnabas troughs (Hollowed et al., 2007; Logerwell, Duffy-Anderson, Wilson, & McKelvey, 2010); therefore, the observed shifts in piscivores may reflect a shift in diet from pollock to capelin coupled with an attempt to balance the metabolic demands imposed by warmer ocean conditions.

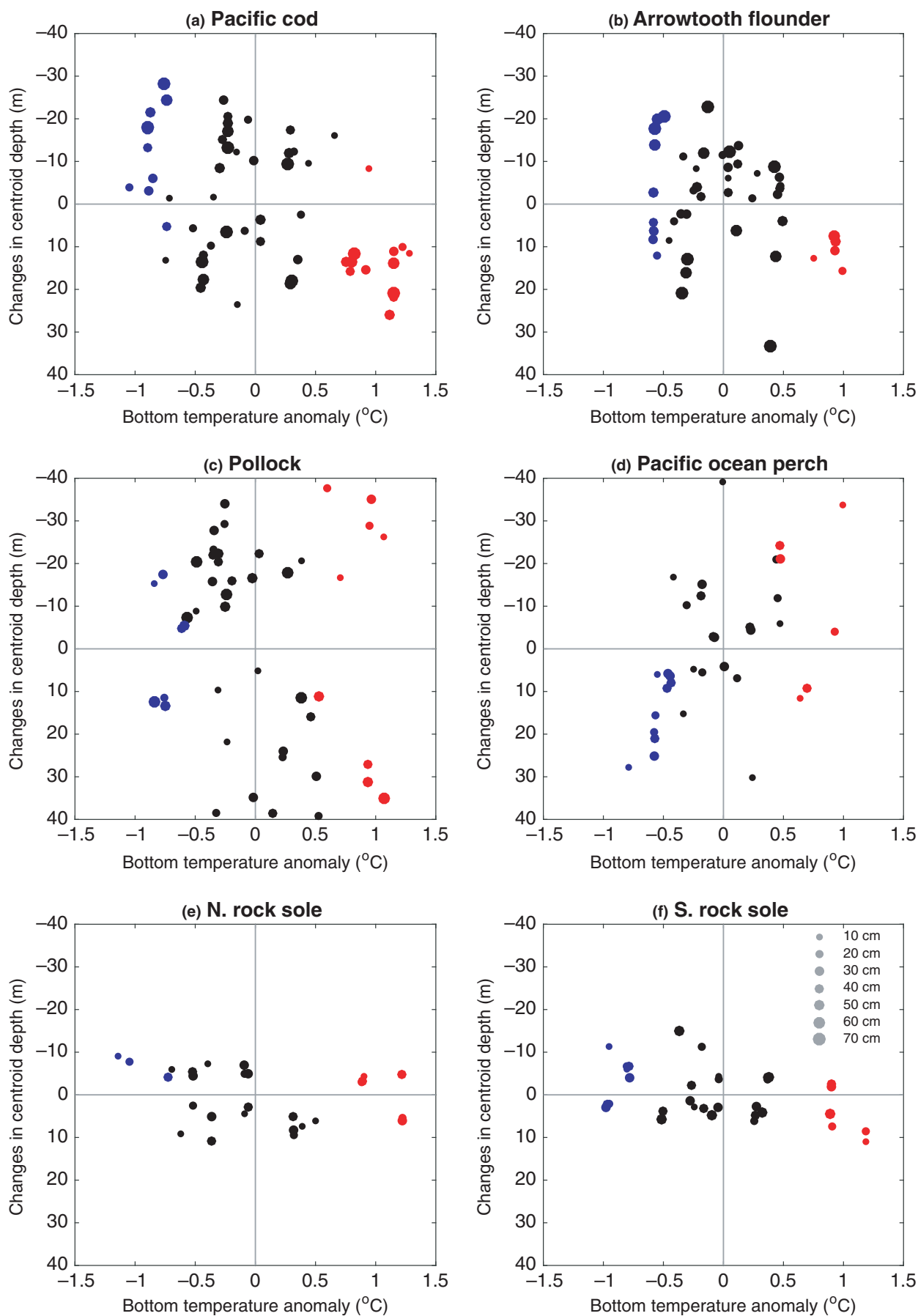
Previous studies in other regions have provided evidence of the dual roles of metabolic demands and prey availability. In the Bering Sea, studies of the arrowtooth flounder showed an on-shelf movement in warm ocean conditions, perhaps following age-0 walleye pollock, which represent a key prey species (Spencer, 2008; Spencer et al., 2016). In the same region, thermal boundaries appear to partition Pacific cod and capelin in cold years, while in warm years thermal gateways provide regions of overlap between cod and capelin (Ciannelli & Bailey, 2005). Age-0 and age-1 pollock may have used high productivity regions in the northern Bering Sea as a refuge from anomalously warm summer ocean conditions in 2015 and 2016

(Duffy-Anderson et al., 2017). In New England, studies of the spatial distribution of two piscivorous species revealed that past fishing pressure and thermal affinities acted to buffer the ecosystem structure to impacts of climate change on distributional changes in piscivorous fish species (Selden, Batt, Saba, & Pinsky, 2018).

The two pelagic planktivore groundfish (walleye pollock and Pacific ocean perch) exhibited different responses to habitat temperature changes. In response to warmer habitat, smaller walleye pollock (10 and 20 cm) were found in shallower waters and larger pollock (>30 cm) in deeper waters. However, there was no clear change in depth-at-size in response to colder habitat. Several processes could explain these results. Small pollock may have fewer options to avoid anomalous ocean conditions if they are restricted to shallower depths by the availability of suitable prey or the absence of predators. Alternatively, the spatial distributions of small-sized pollock in 2013 and 2015, respectively, may have been influenced by the presence of a strong year class entering the population as age-1 in 2013 and a poor year class entering the population as age-1 in 2015 (Dorn et al., 2017). Thorson, Ianelli, and Kotwicki (2017) applied a vector autoregressive approach to center of gravities in a study of spatial patterns of pollock in the Bering Sea and found that neither temperature nor size captured the 1982–2015 northwest shift in the distribution. In their analysis of Bering Sea species, Barbeaux and Hollowed (2018) also found ontogenetic differences in distributional shift with a northward shift for smaller walleye pollock and a shift northeastward and deeper for larger size categories in years with warmer water conditions.

Pacific ocean perch exhibited an opposite response to thermal changes in habitat, compared with Pacific cod and arrowtooth flounder. They moved deeper in colder waters, but no clear change in depth-at-size in response to warmer habitat. This finding may be related to thermal tolerances for this species in conjunction with density-dependent factors. During our study period, the Pacific ocean perch population expanded considerably; therefore, some observed movements may be a result of density-dependent responses to available habitat.

Northern rock sole (a benthivore) tended to move shallower in colder conditions, but no clear movements during warmer periods were observed. Similarly, no noticeable changes in depth distribution at size were found for southern rock sole (a benthivore). Previous studies have revealed that southern rock sole exhibit a restricted depth range on specific substrates (Abookire & Norcross, 1998). Movement to deeper depths to avoid warmer water events may be limited for the two rock sole species because they are mostly



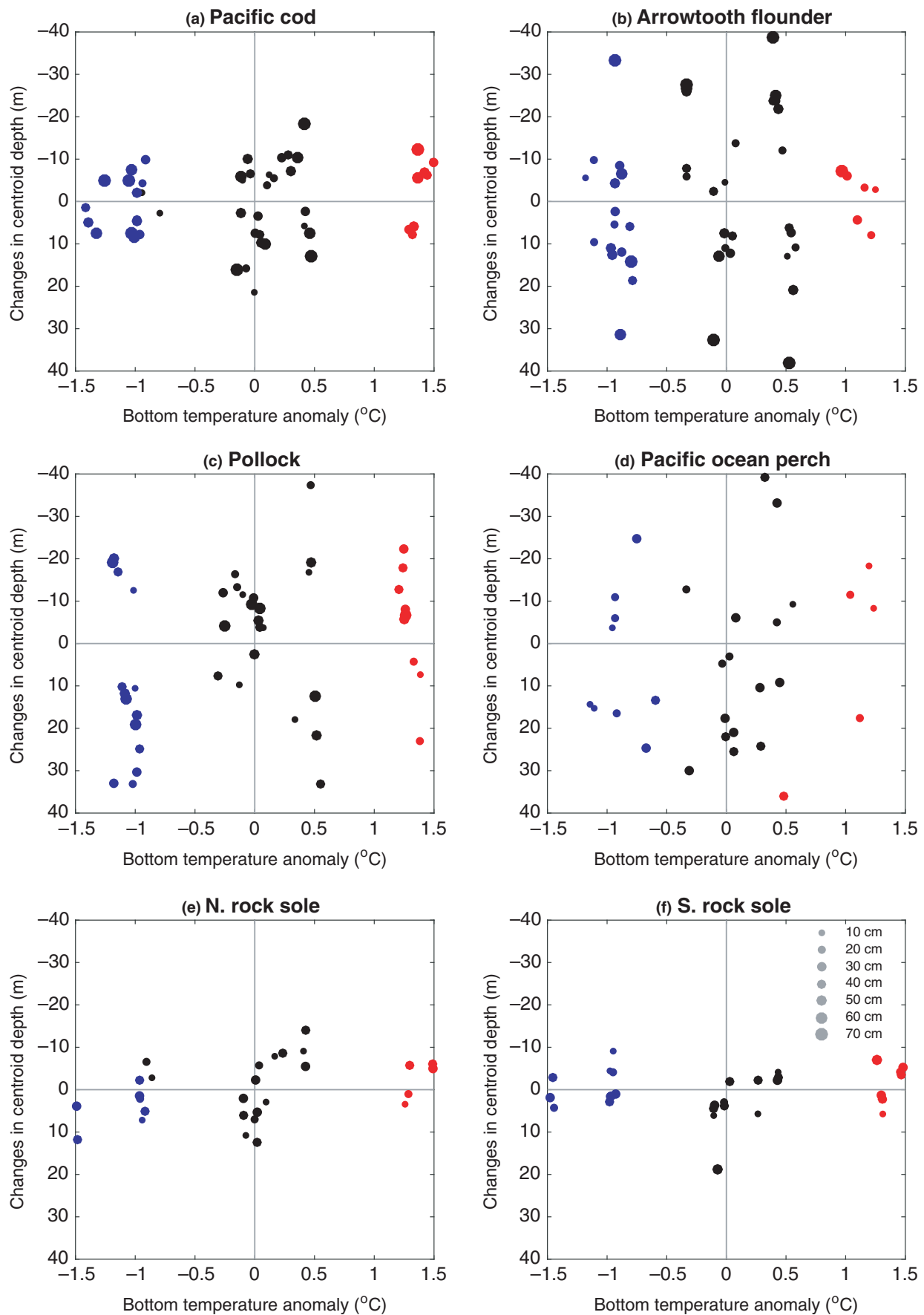


FIGURE 11 Same as Figure 10, but for the western Gulf of Alaska (WGOA) [Colour figure can be viewed at wileyonlinelibrary.com]

distributed in waters <200 m for all settled life stages (Rooney et al., 2018), and therefore may be limited in the extent that they can move with different temperature regimes.

Our main findings support hypotheses presented in the introduction. Large Pacific cod and arrowtooth flounder are piscivorous species that can tolerate a broad bathymetric range. Both species moved to deeper waters perhaps in response to the dual pressures of increased metabolic demands and density of prey. Our study revealed that shallow-water species such as southern rock sole were less responsive to shifting ocean conditions. This finding was consistent with the hypothesis that responses of shallow-water species (<50 m) would be less evident because they are better adapted to variable ocean conditions during summer.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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